We investigated the neural substrates of a recent model of human stereodepth perception by obtaining measurements of regional cerebral blood flow (rCBF) using PET. Subjects experienced the perceptual properties of stereopsis by viewing rival-luminance stereograms displaying an identical random-dot pattern in their central portion while the backgrounds exhibited correspondent dots contrasting in black/white luminance. The stereoscopic vision induced by retinal luminance rivalry coincided with a significant elevation of rCBF in the dorsal visual pathway. Area V5 (MT) was activated bilaterally by the experimental condition while the remaining active loci were restricted to the right hemisphere. The neural sites that responded to this novel stereoscopic stimulus are similar to those activated by traditional stereograms containing horizontal disparities. 

Key words: Area MT; Binocular luminance rivalry; Brain imaging; Human; Stereopsis; Visual areas
consent in accordance with the guidelines approved by Aarhus University and the Montreal Neurological Institute Ethics committees.

**Stimuli:** The subjects were presented two stimulus conditions: Faubert rival-luminance stereograms and a form (control) stimulus. The pair of rival-luminance stereograms contained a central square region showing an identical pattern of random-dots, whereas the surround was comprised of corresponding points displaying opposite black/white luminance (Fig. 1a). The background dots were designed to send rival and non-alternating inputs to the retina, where the binocular coordinates contrasted in terms of luminance. No shape or depth was apparent by looking at the stereograms independently. However, a fusion of the two with the use of red–green glasses produced an illusion of depth in that a square appeared closer to the observer than the surrounding area. The form stimulus consisted of the same stimulus but free of luminance disparities leading to the perception of a monocularly visible square in its center. It hence displayed a different level of luminance relative to the background, but it did not produce the sensation of a 3D surface. Six sets of PET scans (PC-2048B tomograph) were obtained for each participant under both stimulus conditions. To ensure that the rCBF values recorded during the Faubert stereogram presentations reflected only the neural processing of depth information and not the visual inputs related to the form of the stimulus, the responses elicited by the form (baseline) stereograms were subtracted from the metabolic activity derived from retinal luminance rivalry.

**Eye movements:** The subjects’ oculomotor behavior during stimulus presentations was recorded using an infrared video camera (ISCAN, Cambridge, MA) that tracks the center of the pupil and the corneal reflection. Horizontal and vertical movements of the left eye were analyzed dedicated scripts written in Matlab, which allowed us to identify and remove blink artifacts, and subsequently detect and measure the amplitude of saccadic eye movements. Data showed that the number of saccades $>0.5$ and the mean amplitude varied across subjects but did not differ across conditions (Friedman ANOVA, $p > 0.5$), thus ruling out the contribution of eye movements to the observed brain activations.

**Subject preparation and procedure:** Prior to brain imaging, a fine needle-catheter was inserted into the brachial vein for the administration of a radioactive substance with a short half-life ($10 \text{ mCi H}_2^{15}\text{O}$). Three scans were taken during each of the two experimental conditions, yielding a total of 60 CBF volumes. All scans (50s duration) were carried out 10 s of the two experimental conditions, yielding a total of 60

**RESULTS**

The brain areas that were activated by the experimental luminance-based stimulus are depicted in Table 1. The cerebral activity due to the form of the stimulus has been subtracted from the reported values. Rival-luminance stereogram presentations significantly increased rCBF in areas BA 18 and 19 of the right occipital lobe. Two peaks of activation were also apparent in the superior (BA 7) and inferior (BA 40) parietal lobules of the right hemisphere. An elevation in blood flow was further noted in the frontal lobe (area BA 9) and it was specific to the right side of the brain. Activations were also detected in the middle temporal visual area (MT), but these were bilateral. These results are illustrated in Fig. 1.

**DISCUSSION**

We used a pure form of luminance-based stereogram in combination with neuroimaging techniques to examine how the human brain processes rival inputs originating from the retina in order to generate a 3D percept. Our data show that the occipital, parietal and temporal cortices are all implicated in depth information processing. The results further indicate that although MT was bilaterally activated by retinal luminance rivalry, the other cortical regions all demonstrated a right hemispheric dominance, in agreement with the findings of other studies. The results of this study suggest that the visual system is capable of processing rival inputs originating from the retina in order to generate a 3D percept. The neural mechanisms underlying this process are likely to be complex and involve a combination of low-level visual processing and higher-order cognitive functions. Further studies are needed to elucidate the neural basis of the human ability to perceive depth from luminance rivalries.
with earlier reports showing the lateralization of stereoscopic processing in the human brain [8–12].

Our results revealed that the frontal cortex, predominantly in the right hemisphere, is metabolically activated by rival-luminance stereograms. Frontal lobe activity during exposure to stimuli that produce a sensation of depth has also been noted by others investigators [8–11,13]. However, patients who have been subjected to a right frontal lobectomy do not have difficulty extracting depth information from positional disparity-based stereograms [14], suggesting that the frontal cortex is not directly involved in the processing of stereoscopic information. It is interesting to note that sustained attention is associated with increased neural activity in the prefrontal region of the right hemisphere [15,16]. It can therefore be argued that frontal lobe activation during stereoscopic stimulation is simply an indicator of the attentional requirements of the visual task as opposed to a true representation of stereodepth information processing.

We show for the first time that the depth information derived from retinal luminance rivalry is treated in the same regions of the human brain as that generated by random-dot stereograms containing horizontal disparities [8–13,17,18]. The neuronal components of the occipital, parietal and temporal lobes that are activated by luminance and positional disparity-based stimuli constitute the occipitoparietal pathway or dorsal stream, which is known to play a crucial role in spatial perception [19]. The brain regions comprising this dorsal pathway appear to be hierarchically organized (in monkeys, [20] and in humans [8,21–24]) in that the visual inputs originating from V1 are sequentially processed in V2, V3, MT, the medial superior temporal area and finally the parietal cortex.

In conclusion, we show that the anatomical structures of the human brain that mediate stereoscopic vision form a neural pathway comprising areas in the occipital, parietal and temporal cortices. Our data provide strong evidence to show that stereodepth analysis are primarily carried out in the right cerebral hemisphere. The findings further demonstrate that the cortical neurons implicated in depth perception can be activated by visual inputs that are disparate in terms of luminance or their spatial location on the retina. It would now be interesting to demonstrate with single-cell recordings that the neural elements selectively activated by binocular horizontal disparity also respond to retinal luminance rivalry.

Fig. 1. Active brain sites after the form of the stimulus has been accounted for. (a) Coordinates (derived from the sections in b) of activated cortical regions are placed on 3D cerebral hemispheres. The luminance-based stereogram is on the right. (b) Sections showing the activation sites (arrows).
REFERENCES


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